Phylogeny of the Non-Aculeate Apocrita and the Evolution of Parasitism in the Hymenoptera

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Abstract.— Recent interest in the higher-level phylogeny of Apocrita has led to the advancement of several competing hypotheses of relationships among major lineages. Nevertheless, some areas of agreement do exist among these hypotheses, providing a base from which further progress can be made. A well-corroborated phylogeny for the Apocrita would be extremely useful for interpreting the evolution of parasitism, among other features, within the Hymenoptera. Comparative studies of parasitoid/host biology are still at a relatively early stage. Most of what is known of parasitoid biology is derived from relatively few taxa of Ichneumonoidea, Chalcidoidea and Scelionoidea, and even within these groups data are extremely sparse. A number of specialized biological features associated with endoparasitoid groups show intriguing patterns of distribution among taxa, but so little is known of these features across all taxa that coherent evolutionary hypotheses concerning these features cannot yet be advanced. It is suggested that more emphasis be given to *comparative* parasitoid biology, especially within poorly-known groups.

Interest in the evolution of the Hymenoptera is certainly not new; broad treatments of the phylogeny of the order and the evolution of the food habits of its members span at least most of this century (e.g. Handlirsch 1907, Börner 1919, Bradley 1958, Malyshev 1968, Iwata 1976, Tobias 1976, Hennig 1981). Only within the past several decades, however, have relatively explicit and practical methods of phylogenetic inference been available so that studies of hymenopteran evolution have become repeatable and open to productive criticism. Even more recent is the wholesale recognition of the value of specific phylogenetic hypotheses for interpreting the evolution of biological traits (e.g. Coddington 1988, Donoghue 1989, Brooks and MacLennon 1991, Harvey and Pagel 1991).

Although this by no means implies that studies of hymenopteran evolution prior to the last few years do not continue to be valuable (such careful studies as those of Oeser 1961 and Brothers 1975 on Aculeata, for instance, have held up remarkably well to further scrutiny), it is much easier to evaluate the more recent ones in the light of the actual evidence that is presented, so that one study builds upon another.

In this brief overview I first hope to quickly cover some of the major findings and controversies of recent phylogenetic studies of the higher taxa of Hymenoptera, focusing especially on the non-aculeate Apocrita, which were often under-represented and poorly understood in earlier studies. I will begin with the exhaustive literature review and analysis of Königsmann (1976, 1977, 1978a,b) and continue to the present, attempting to consolidate some areas of agreement among the various studies and to point out where disagreement is rampant and further study would be most valuable.

In the second main segment of this paper I briefly review what is currently known about various comparative aspects of the parasitoid habit among the groups of non-aculeate Apocrita. I will first focus on the ways in which parasitoids have overcome the problems associated with an evolutionary transition from ectoparasitism (the putative ancestral form of parasitic lifestyle in Hymenoptera) to endoparasitism. There will follow a brief discussion of how some of these parasitoid "strategies" are distributed among hymenopteran higher taxa. Although an attempt will be made to illustrate the value of a phylogenetic perspective in interpreting such comparative data, the major goal of this review is to point out areas where new comparative biological data would add appreciably to our understanding of the evolution of parasitism in the Hymenoptera. It is one major virtue of a phylogenetic approach that the distribution and depth of comparative data among taxa must be made explicit so that areas of ignorance become clear.

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RECENT PHYLOGENETIC STUDIES
OF APOCRITA

Königsmann (1976, 1977, 1978a,b) compiled a large, predominantly morphological, data set from the literature, for phylogenetic analysis of higher-level relationships within the entire order Hymenoptera. His analyses, although rigorous and based on the largest data set produced to that time for hymenopteran phylogeny, suffered from the lack of sufficient characters for many groups, partly because he did not contribute new ones but also because the data set did not include a number of characters already evident to other workers for various groups. Nevertheless, his study did represent perhaps the first rigorous attempt to analyze relationships within the order, and served to highlight the lack of knowledge of, and lack of resolution among, most of the non-aculeate apocritan groups. Figure 1 represents his findings for the Apocrita in an abbreviated form. It is of some significance that his data appear not to support the monophyly of any non-aculeate apocritan groupings above the superfamily level (other than the somewhat controversial one of Evanioidea + (Cynipoidea + Chalcidoidea)), nor of the monophyly of the traditional Proctotrupoidea. Masner and Dessart (1967) had already suggested that the Ceraphronoidea should be recognized as a separate superfamily, but the inability of the avaliable data to support the monophyly of the remaining taxa was somewhat surprising. In addition, Königsmann's analyses suggested that the extant sister-group to Apocrita was most likely the Cephoidea, as Malyshev (1968), among others, had suggested.

The next major set of contributions to apocritan phylogeny were made by Rasnitsyn (his papers of 1980 and 1988 most relevant to the present discussion). In addition to a more thorough knowledge of comparative morphology across many groups, Rasnitsyn's work included comprehensive consideration of the available fossil evidence, much of which had rarely been examined by workers outside of the USSR. Although the details of his phylogenetic hypotheses and classifications evolved somewhat over the years, his 1988 paper largely summarizes the others and provides a concise introduction to the evidence he uses to support his phylogeny. A simplified version of his cladogram of the Apocrita (redrawn and omitting extinct taxa) is provided in Figure 2; Figures 3 and
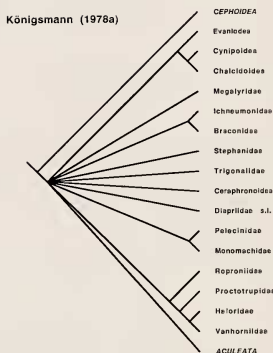

Fig. 1. Cladogram of non-aculeate Apocrita modified from Königsmann (1978a). Note especially the almost complete lack of resolution among the basal branching in the suborder.

4 represent his phylogenetic views on subsets of taxa from Figure 1.

Rasnitsyn's (1980, 1988) cladogram was the first comprehensive, essentially fully resolved phylogenetic hypothesis for the non-aculeate Apocrita that utilized the principle of grouping on the basis of shared derived features. He produced some radical changes in the higher classification of Hymenoptera, several of which are still controversial. His classification suffers from two major weaknesses: 1) his philosophy of classification allows phenetic distinctness to override the strict phylogenetic branching sequences, so that paraphyletic groups are preserved if distinct enough from monophyletic sub-assemblages, and 2) he did not make use of automated searches for most parsimonious trees, so that alternative explanations of the data were often not considered. Nevertheless, his work marked a major progressive step in the study of hymenopteran phylogeny. To a large extent, most subsequent studies have focused on

Rasnitsyn (1988)

- other Siricoidea
- Xiphydriidae
- Orussomorpha
- Ichneumonomorpha *(Ichneumonoidea)*
- Vespomorpha *(Aculeata)*
- Proctotrupomorpha *("Microhymenoptera")*
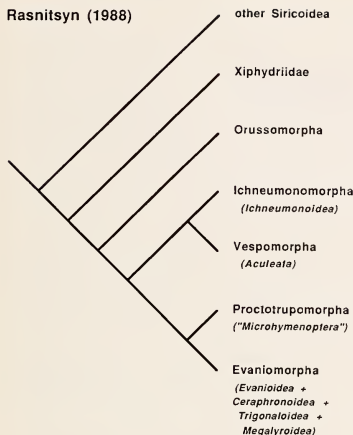- Evaniomorpha *(Evanioidea + Ceraphronoidea + Trigonaloidea + Megalyroidea)*

Fig. 2. Cladogram of major lineages of non-aculeate Apocrita greatly modified from Rasnitsyn (1988). Fossil taxa have been deleted from this representation of his work, and several putative monophyletic groups have been collapsed into single units. Figures 3 and 4 are more detailed treatments of parts of this figure.

testing his ideas and, to date, no comprehensive study has yet superceded his.

Rasnitsyn (1980, 1988) established clearly that the extant sister group to the traditional Apocrita is the Orussidae, a relationship that virtually all subsequent studies (e.g. Gibson 1985, Johnson 1988; Whitfield et al. 1989) have confirmed and that provides a direct biological link between the Symphyta and the parasitoid habit among the Apocrita. Secondly, he proposed two large groupings below the level of suborder that were not previously recognized: the Proctotrupomorpha (Fig. 3 - Chalcidoidea + Proctotrupoidea s.l. + Cynipoidea + Scelionoidea) and the Evaniomorpha (Fig. 4 - Evanioidea + Ceraphronoidea + Trigonalyidae + Megalyridae + Stephanidae). His Ichneumonomorpha corresponded to the traditional Ichneumonoidea and the Aculeata, as recognized by Oeser (1961) and Brothers (1975), remained with its usual boundaries. Of his novel findings, the Evanioidea is the most controversial grouping, in particular the inclusion within it of Stephanidae and Trigonalyidae. Al-

though some relationships within this proposed higher taxon have been supported by subsequent studies (Johnson 1988), morphological evidence now suggests (Gibson 1985, Johnson 1988, Mason, unpublished) that the Stephanidae occupy an extremely basal position within the Apocrita and are not closely related to the other "Evaniomorpha". The Proctotrupomorpha grouping has been supported in large measure by the comparative skeletomusculature studies of W.R.M. Mason (unpublished, there treated as the "Micro-hymenoptera").

Although no single study has superceded that of Rasnitsyn (1980,1988), the accumulation of additional comparative morphological studies along the lines of Gibson (1985,1986) on thoracic skeletomusculature, Johnson (1988) on mesotharacic skeltomusculature and midcoxal articulations, Robertson (1968) on venom apparati, Darling (1988) on the labrum, Whitfield et al. (1989) on the metapostnotum and associated musculature, and the ongoing studies by W.R.M. Mason (in preparation, featuring especially the mesosomal-metasomal articulation and musculature) will clearly be helpful in further resolving higher relationships within
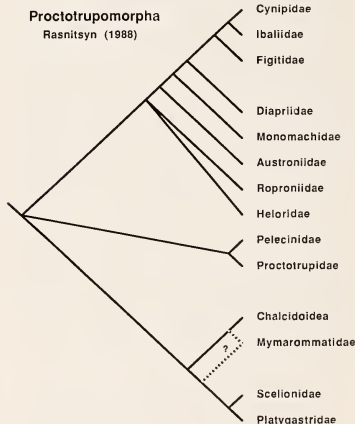
Proctotrupomorpha
Rasnitsyn (1988)

- Cynipidae
- Ibaliidae
- Figitidae
- Diapriidae
- Monomachidae
- Austroniidae
- Roproniidae
- Heloridae
- Pelecinidae
- Proctotrupidae
- Chalcidoidea
- Mymarommatidae
- Scelionidae
- Platygastridae

Fig. 3. Rasnitsyn's (1988) hypothesis of relationships among the "Proctotrupomorpha". The uncertain relationship of Mymarommatidae (but see Gibson 1986) is denoted by dotted lines; otherwise, lack of resolution is indicated by polytomies.

the Apocrita, as will molecular systematic studies now still in their early stages (see elsewhere this issue). Care must be taken, however, to include many of the less easily available taxa, such as Megalyridae, Stephanidae, Trigonalyidae and Orussidae, since these have proven to be critical taxa in determining the larger phylogenetic patterns especially in the early evolution of Apocrita.

HYMENOPTERA AS PARASITOIDS

If the Orussidae are the sister-group to the Apocrita, as is presently best supported by the available evidence, the parasitoid habit may have had a single, unique origin within the Hymenoptera - in the common ancestor of Orussidae and Apocrita. The biology of orussids is poorly studied, but what is known is consistent with ectoparasitism of xylophagous Coleoptera, with the egg laid near the (possibly envenomated) host (Cooper 1953, Powell and Turner 1975, Gauld and Bolton 1988). This biology is remarkably similar to that of basal lineages of Ichneumonoidea, Evanioidea (albeit at least some Aulacidae are apparently endo-parasitoids), Stephanidae and Megalyridae. It is also not terribly different in the host/parasitoid relationship to that of basal groups of Aculeata.

Some sort of ectoparasitic habit, therefore, appears to be a groundplan state for many (but not all —note the apparent absence of any extant ectoparasitoids among the Cynipoidea, Scelionoidea and Proctotrupoidea *s.l.*) of the major apocritan lineages. Although many variations of behavior and host-parasitoid interaction do exist among ectoparasitoids, and these are of considerable phylogenetic interest as well, it is among the endoparasitoids that the most extreme elaborations of parasitoid habits have been developed. I would like to focus on what currently can be postulated of the evolution of these various forms of endoparasitism, based on what is known of comparative parasitoid biology, and what is known, or hypothesized, of the phylogeny of the Apocrita. But first a brief discussion of what it means to be a hymenopteran endoparasitoid.

THE PROBLEMS OF ENDOPARASITISM

It has been apparent for some time that the condition called "endoparasitism" is really a collection of different biological relationships, all of which share the feature of the parasitoid feeding from entirely inside the host organism, rather than from the outside.

Evaniomorpha
Rasnitsyn (1988)

- Stephanidae
- Megalyridae
- Trigonalidae
- Megaspilidae
- Ceraphronidae
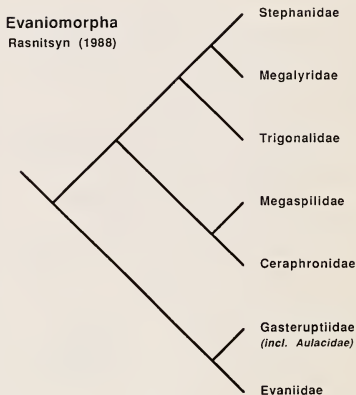- Gasteruptiidae *(incl. Aulacidae)*
- Evaniidae

Fig. 4. Rasnitsyn's (1988) hypothesis of relationships among the "Evaniomorpha". Note his inclusion of Trigonalidae and Stephanidae in this assemblage.

Many of the features usually associated with endoparasitism are actually associated more closely with koinobiosis (Askew and Shaw,1986; Gauld, 1988; Gauld and Bolton, 1988). This refers to a prolonged, complex interaction with the host (and in endoparasitoids this is with the internal milieu of the host), in contrast to the rapid feeding on moribund hosts more often found in ectoparasitoids (idiobiosis). Some of the most physiologically complex interspecific interactions known to science are between endoparasitic koinobionts and their host organisms, and many of the details of even the best-known cases are not fully elucidated.

There are major evolutionary problems to be solved in any transition from ecto- to endoparasitism, or from idiobiosis to koinobiosis. The defense reactions of the host insects, especially the cellular responses (Götz 1986, Lackie 1980, Nappi 1975, Salt 1968, 1970) must be overcome once the transition is made to development within host organisms. The parasitoid may have to control the physiology of the host to some extent (Beckage 1985, Jones 1985, Lawrence 1986, Stoltz 1986, Vinson and Iwantsch 1980b), or it must prevent the hormonal milieu of

the host from controlling its own physiology, or at least use the host's physiological signals to its own advantage (Lawrence 1986, Jones 1985).

The solutions to these problems in endoparasitoids appear to have varied greatly from group to group, depending on the options open to them during their evolutionary history. In a few cases the parasitoid may be able to avoid some of the above problems by placing its egg in particular host tissues, or by insulating itself in some way. In at least one species of *Eretmocerus* (Chalcidoidea), the parasitoid larva, although technically an endoparasitoid, is encased within a capsule that protects it from the internal milieu of the host (Gerling et al. 1990). In most cases, however, more direct interaction with the host is encountered, and parasitoids have a number of "tools" at their disposal for dealing with this interaction. For instance, many ectoparasitoids use a *venom* to temporarily or permanently paralyze the host (Beard 1978, Piek and Spanjer 1986, Steiner 1986). The evolution of this paralytic venom is an interesting problem in itself. Even phytophagous Siricoidea and Cephoidea secrete compounds (whether homologous or not) that influence either the host plant or fungal associates of the host plant in ways that benefit the developing wasp larva. How the first paralytic venoms might have arisen from any such possible precursors is not known, as comparative biochemical analyses of venoms and associated substances are still in their early stages. The neurotoxic and preservative effects of the paralytic venoms of parasitoids are of considerable pharmaceutical interest, but have not yet been capitalized upon. There are some chemical similarities between some components of these venoms and components of the more well-studied venoms of the social Hymenoptera (for a review of comparative aspects, see Piek 1986 and Leluk et al. 1989), as should be expected since the ancestral biology of Aculeata is ectoparasitism.

In endoparasitoids the venom may retain a paralyzing function, or be adapted to influence the host physiology in some way, or act in both ways, or neither (Shaw 1981, Piek and Spanjer 1986, Steiner 1986, Stoltz 1986). Leluk et al. (1989) have shown that the venom of many endoparasitoids contains large protein components not found in the paralytic venoms of ectoparasitic Apocrita. In addition, a number of interactions between venoms and other parasitoid-derived products have been reported (Stoltz 1986, Stoltz et al. 1988, Tanaka and Vinson

1991a,b), so that the extent of host modification or regulation that can be directly attributed to venom is relatively poorly known, and for only a few taxa. The problem is clearly a complex one, but future surveys of venom components from groups in which the phylogenetic relationships and host/parasitoid biologies are known may suggest functions for some of the venom proteins and aid in the understanding of the biochemical aspects of host/parasitoid interactions (Leluk et al. 1989). In this respect, comparative systematic studies of venom gland structure, as begun by Edson and Vinson (1979) and Edson et al. (1982) may also provide initial insights into venom functions even before biochemical analyses are undertaken.

In many braconids and assorted other parasitic Hymenoptera (see below), the serosa or trophamnion associated with the parasitoid egg appears to facilitate the uptake of nutrients by the developing embryo, and may fragment into individual free-floating cells variously called teratocytes (Salt 1968, Vinson 1970, Vinson and Iwantsch 1980b, Dahlman 1990) or "giant cells" (Jackson 1935, Gerling and Orion 1973), among other names. That some kind of nutritive function is served by these teratocytes has been suspected by many workers, but other functions attributed to them, such as production of juvenile hormone (Vinson 1970, Joiner et al. 1973) or fungicidal activity (Führer et al. 1978), dissolution of host tissues (Mackauer 1959, Sluss 1968, Gerling and Orion 1973) or overwhelming of the host's cellular defenses (Salt 1968, 1970), are less well established and require much further investigation (Vinson and Iwantsch 1980b, Stoltz 1986). However, at least the juvenilizing effects are being corroborated by recent work (Strand and Wong 1991). It is not clear that "teratocytes" are a homologous phenomenon in all of the parasitoids studied; much further comparative morphological and developmental work is required. An additional complication for such studies will be that in some species, teratocytes may be diversifying into different types with age (Strand and Wong, 1991).

In some endoparasitoids, *viruses* associated with the adult female wasps are injected with the eggs, either aided or not by venom effects. These viruses can effectively suppress the immune system of the host as well as cause some other physiological changes (Rotheram 1967, Stoltz and Vinson 1979, Faulkner 1982, Beckage 1985, Blissard et al. 1986, Stoltz 1986, Guzo and Stoltz 1987, Jones 1987, Dover et al. 1987, 1988, Schmidt and Theopold, 1991).

Recent studies indicate that at least some of these viruses are integrated into the wasp genomes and are inherited from mother to offspring (Stoltz et al. 1986, Fleming and Summers 1986, Stoltz 1990). The predominant group of viruses that has been studied are the polydnaviruses, of two rather distinct (and probably distantly, if at all, related) types associated with some subfamilies of Ichneumonidae and Braconidae, respectively. Other kinds of viruses are known to be associated with parasitoid ovaries or venom glands, however, and may be of greater significance than is currently realized (Edson 1981, Stoltz 1981, Lawrence and Akin 1990, Rizki and Rizki 1990). A more comprehensive overview of the associations between parasitoids and viruses is presented elsewhere in this issue (Stoltz and Whitfield 1992). Inheritance (strictly vertical transmission) suggests that at least some virus strains and their relationships should correlate with the phylogenies of the wasps themselves, providing an example of how knowledge of the phylogenetic relationships of the parasitoids can guide lines of productive research in other areas. It should be possible, using modern molecular genetic techniques and co-phylogenetic approaches (e.g., Page 1990, 1991, Brooks and McLennan 1991) to investigate the coevolution between the wasps and viruses and their evolutionary interactions with host organisms. Some initial efforts are already being made along these lines (Cook and Stoltz 1983, Whitfield 1990, Stolz and Whitfield 1992).

Host/parasitoid physiological interactions are quite complicated syndromes of behaviors and phenomena (Fisher 1971, Vinson and Iwantsch 1980a, 1980b, Jones 1985, Lawrence 1986, Strand and Wong 1991, Thompson 1983, 1990) that might also be found to show phylogenetic trends, independent of whether the precise "tools" the parasitoids and hosts use to effect them can be elaborated. Variations occur in whether host ecdysis and development from one instar to another are possible, and in whether the parasitoid larva uses host hormonal levels to time its own development (Beckage 1985, Lawrence 1983, Shaw 1983). Parasitoid groups might be found to have general requirements for survival that can be satisfied in different specific ways depending on the host group being attacked. Whether any given interactive endocrine response is selectively advantageous in its current situation or whether it has been inherited as a part of a syndrome from distant ancestors (or both) is seldom known, but could perhaps be ap-

proached with additional comparative data. Integration of phylogenetic relationships of parasitoids with information gleaned from repesentative study organisms should help to clarify the evolutionary significance of many of these host/parasitoid endocrine interactions. However, one major caveat should be added about the use of phylogenetics in interpreting the evolution of complex biological habits. The success of any phylogenetic study depends not only upon the accuracy of the biological information put into it, but also upon the sensible division of the often complex biological features into independent, unitary character states. In this respect, detailed comparative studies of the biologies of related organisms, such as those done by Shaw (1983) and Whitfield (in press), may prove a crucial step in the elucidation of more complex evolutionary sequences.

Relatively little can be said definitively about the evolution of various parasitoid habits among the Hymenoptera until more well-defined phylogenetic relationships are known and considerably more comparative biological data is available. However, I attempt below to briefly touch upon what patterns can been seen by reviewing of the literature on apocritan parasitoids, focusing particlarly on the distributions of venom types, viruses and teratocytes among endoparasitoids. It will quickly become obvious that few conclusions should be drawn from the information presently available. Nevertheless, the exercise may be useful in suggesting areas where further information is especially needed.

PHYLOGENETIC TRENDS IN HOST/PARASITOID BIOLOGY

It has been remarked upon above that the groundplan biology for many of the apocritan lineages is a form of ectoparasitism marked by oviposition on or near a partially or totally incapacitated host, usually in a concealed situation. For each infraorder discussed below, I will briefly touch upon the extent to which this groundplan biology is still found in the group, and in what major ways divergence has occurred from this groundplan within the group. Repeated reference to Table 1, which shows the distribution (if known) among taxa of a persistent trophamnion, teratocytes and/or viruses that may affect the host, may be useful as a quick reference for endoparasitoid taxa when some aspects of host/parasitoid biology are being
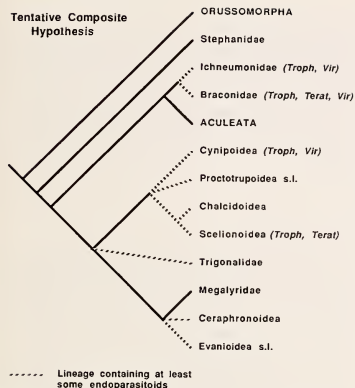
Tentative Composite Hypothesis


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                              ORUSSOMORPHA

                          Stephanidae

                      Ichneumonidae (Troph, Vir)

                      Braconidae (Troph, Terat, Vir)

                    ACULEATA

                  Cynipoidea (Troph, Vir)

                  Proctotrupoidea s.l.

                  Chalcidoidea

                  Scelionoidea (Troph, Terat)

              Trigonalidae

          Megalyridae

        Ceraphronoidea

      Evanioidea s.l.
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- - - - - -   Lineage containing at least
               some endoparasitoids

Fig. 5. Composite hypothesis of apocritan relationships, based largely on Rasnitsyn (1988) but modified based upon findings by Mason (unpublished), Gibson (1985), Johnson (1988) and Whitfield et al. (1989). Lineages marked as containing endoparasitoids may also contain (often among their basal clades) some ectoparasitoids. **Troph** - presence of a persistent trophamnion, at least through first instar, in at least some species. **Terat** - presence of some sort of teratocytes in at least some species. **Vir** - presence of some sort of associated viruses (that are introduced into host insects) in at least some species. Not all species in lineages marked with these abbreviations necessarily, nor are all occurrences of a trophamnion, teratocytes or viruses assumed to be homologous. Apparent absence of a trophamnion, teratocytes, or viruses in a lineage may be simply due to lack of data in many cases. Both the tree and the distribution are offered to suggest groups in which further research would be especially helpful.

discussed. Figure 5 shows the phylogenetic distribution of the presence of these features, as superimposed upon a "composite cladogram" concocted from the hypothesis of Rasnitsyn (1988) combined with refinements by other concurrent and subsequent research (e.g. Mason upublished, Gibson 1985, 1986, Johnson 1988, Whitfield et al. 1989).

"Ichneumonomorpha "

The ectoparasitoids found within basal lineages of both Ichneumonidae and Braconidae appear to fit the general groundplan biology in possessing paralyzing venoms for incapacitating hosts (the venom of *Bracon* being the best-studied example - see Beard 1978 and Piek 1986 for more details) and and rapid development of the larvae upon the usually moribund host. Within each of these two families some form of endoparasitoid habit has appeared several times (see Gauld 1988 for overview; Shaw 1983 and Whitfield, in press, provide a relatively well-studied example from the Braconidae). Within each of the two families a number of derived features associated with endoparasitism have independently appeared in remarkably similar fashion - a prominent case being the existence of mutualistic viruses asociated with immune suppression of hosts in microgastrinae and chelonine and related braconids and in campoplegine and a few other ichneumonids. There is no real indication, however, that the ichneumonid-associated viruses and the braconid-associated viruses are particularly closely related, let alone form a monophyletic group.

Gauld (1988) has pointed out some differences between the two families in evolutionary trends in parasitism, especially in the host groups exploited and in what way they are utilized. An additional difference that appears from a review of the literature is that many braconids possess teratocytes that influence the host/parasitoid relationship, whereas ichneumonids are not known from Ichneumonidae. Nevertheless, I expect that this trend will be found to hold only at some level lower than the family level, since teratocytes appear to be absent from many endoparasitoid braconids and few ichneumonids have been intensively studied enough to rule out the existence of teratocytes during their development.

In both families, but particularly in Ichneumonidae, some endoparasitoids of host pupae are found that apparently do not interact in a particularly active or long-term way with the host and show little biological similarity to the more derived larval endoparasitoids, as Gauld (1988) has pointed out. In this respect they are similar to the egg parasitoids found in other superfamilies.

Despite the large gaps in our knowledge of comparative biology of Ichneumonoidea, this group is certainly biologically the *best*-known of major non-aculeate apocritan groups, at least in terms of the intimate details of host-parasitoid biology. Nevetheless, much of what is known has been studied in only a few taxa, e.g. Microgastrinae, Aphidiinae and Campopleginae.

"Proctotrupomorpha"

Within this infraorder true ectoparasitoids are found, to my knowledge, only within some groups of Chalcidoidea (especially some or many Chalcididae, Eurytomidae, Torymidae, Eupelmidae, Pteromalidae, Eulophidae and Elasmidae). A number of other groups within Chalcidoidea and Scelionoidea parasitize insect eggs and are not particularly highly derived in their adaptation to endoparasitism, although a few unique venom-associated substances and functions are known (Strand 1986). Nevertheless, the diversity in host/parasitoid biology within this infraorder is truly incredible, ranging from ecto-to endoparasitism, solitary to gregarious and polyembryonic development, spanning a highly diverse array of host organisms; it is difficult to generalize about trends in the evolution of parasitism. Even within some large families such as Pteromalidae, Eulophidae and Encyrtidae, the diversity of lifestyles is bewildering. Although some detailed comparative work has been undertaken on egg parasitoids (especially *Trichogramma* and Scelionidae - e.g., see Strand 1986 and Strand and Wong 1991 for some comparative review), the twin difficulties of poorly known biology (at least at the level of detailed host/parasitoid interactions) and still unsatisfactory (but very rapidly improving) classification for many groups of "Proctotrupomorpha" have hindered comparative work. The potential for significant study of the evolution of parasitism in this infraorder is enormous

A few generalizations can be made. Many of the ectoparasitoids within the Chalcidoidea appear to possess paralyzing venoms and exhibit rapid development within the host organism, as is the general plesiomorphic rule for apocritans. Some of the less derived endoparasitoids, such as the Ibaliidae in the Cynipoidea, appear to possess a final ectoparasitic feeding phase, which might be relatively plesiomorphic, as has been suspected in some braconid groups (Shaw and Huddleston 1991). Within the Chalcidoidea, Proctotrupoidea *s.l.* and Platygastridae some spectacular larval developmental modifications have evolved, the functions of which are not always understood, but appear to be characteristic of phylogenetic lineages. In general, the Proctotrupoidea as a group appear to be relatively less derived in their methods of endoparasitism, but details of their host/parasitoid interactions are sketchy. The equally, if not

even more, poorly-understood parasitic Cynipoidea sporadically exhibit some unusual features, such as mutualistic viruses analogous to those of Ichneumonoidea (Rizki and Rizki 1990), but too little is known of most species to generalize in any significant way about them. Table 1 provides some indication of how little we know currently of some aspects of proctotrupomorph host/parasitoid biology.

"Evaniomorpha"

As discussed above, recent research indicates that this infraorder from Rasnitsyn's (1988) classification is probably not a monophyletic group. Hence, there is perhaps little reason to suspect it to have any biological coherence, even when it is better known biologically. Whatever similarities the Stephanidae and Megalyridae might have, for instance, in ectoparasitism of concealed xylophagous insects, are probably ancestral states shared with many other basal lineages of Apocrita.

The only true endoparasitoids found within this group are within the Trigonalyidae, Ceraphronidae (but not the Megaspilidae) of the Ceraphronoidea, and the Aulacidae of the (possibly also not monophyletic) Evanioidea. The details of the host/parasitoid interaction in these endoparasitoid groups is extremely poorly known and they appear to have little in common with one another biologically. Other groups, such as the Evaniidae and Gasteruptiidae, are hardly parasitoids at all, the former perhaps being better described as predators of cockroach eggs and the latter as consumers of solitary bee larval provisions (and sometimes also of bee larvae). It is possible that the largely hyperparasitic biology of the Trigonalyidae (reviewed by Weinstein and Austin 1991) could ease the difficulties of development of endoparasitoid life in this group, in that they often attack hosts whose immune systems have already been compromised by other parasitoids. No really complex host/parasitoid physiological phenomena have been described in this complex of Hymenoptera, but so little is known that the discovery of such phenomena would not be surprising.

FUTURE RESEARCH

The above brief survey of apocritan parasitoid biology is not a complete review of the subject. The interested reader is referred instead to the more

Table 1. Taxonomic distribution of some "tools" used by endoparasitoids in interactions with host insects. Refer to text for further explanation (especially for those portions of the table where question marks appear). Although space does not permit an exhaustive listing of supportive references here, most sources of information are cited in the text; where essentially nothing is known, a "?" appears; where conflicting or inconclusive reports are available, a "+?" or "–?" appears.

	Trophamnion	Teratocytes	Viruses
Ichneumonomorpha			
Ichneumonidae	+	–	+ (some)
Braconidae	+	+ (some)	+ (some)
Proctotrupomorpha			
Cynipoidea	+	–	+ (some)
"Proctotrupoidea"	–	–	– ?
Chalcidoidea	– ?	– ?	– ?
Scelionoidea	+	+	– ?
Evaniomorpha			
Megalyroidea	–	–	–
Trigonalidae	?	–	– ?
Ceraphronoidea	– ?	– ?	– ?
Evanioidea	–	–	–

comprehensive treatments of Clausen (1940), Askew (1971), Fisher (1971), Vinson and Iwantsch 1980a,b, Thompson (1983), Beckage (1985), Lawrence (1986), Slansky (1986), Stoltz (1986), Gauld and Bolton (1988), Coudron (1990) and Thompson (1990). This review is offered more as a stimulant to further comparative work on parasitoid biology, using the phylogeny of the groups, as far as is known, as a guide. I hope to have demonstrated some areas and groups where further information is most needed, but there really are no biologically well-known higher taxa represented here. Recent developments in physiology, molecular genetics, immunology, cell culture and many other areas now make some aspects of comparative parasitoid biology approachable for the first time. The potential of the parasitic Hymenoptera, both as biological systems for the study of parasitism and as subjects of evolutionary research, has still barely been tapped, relative to the wealth of information that lies yet undiscovered.

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